

Modular cephalic differences among European and African taurine cattle

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ABSTRACT

Aim: The study was aimed to study integration and modularity and specifically addressing two different shaped skull changes associated to different taurine groups and skull modules involvement

Method and materials: It was studied 46 skulls by applying 2D geometric morphometrics methods. Skulls belonged to adult individuals classified into three geographical groups (Occidental Europe n=30, Oriental Europe n=6 and African n=10), although this research does not intend to classify breeds on a phylogenetical point of view, but rather consider anatomical changes among bovine domestic populations from different geographical areas. The original data-size corrected data was analysed with a two discrete modules hypothesis: neurocranium ("braincase") and splanchnocranium ("face").

Results: A clear modularity in skull was seen, being the shape changes more clearly associated with neurocranium, which discriminated better all three groups. These results showed that skull morphometry can separate cattle geographical groups from each other to a great extent and mainly based on neurocranium features.

Conclusion: It was concluded that the neurocranium and the splanchnocranium represent separated modules were confirmed by the different biological information they provided.

Keywords: *Bostaurus Taurus*, cranial morphology, integration, Kuri cattle, phenotypic covariance.

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Introduction

Cattle breeds display extensive morphological diversity (Porter 1991, Pellegrini 2004, Porter et al. 2016) reflecting adaptation to different habitats and productive purposes and their formation is situated between genotype the ultimate source of phenotypic variation and phenotype –upon which selection (natural and artificial) acts- (Renaud et al., 2010). Since the early domestication of cattle, reproductive isolation promoted divergence by genetic drift and natural selection (Jordana, Pelegrín, and Piedrafita 1991). Later on, selective breeding to meet human needs for desired behavioral or physiological traits, such as agricultural work, milk and meat production, resulted in a wide range of morphological variation (Flori et al. 2009). So cattle, like other domesticated species, have been shaped into many morphological types.

Great differences among cattle breeds can be found in the skull, as a reflex of the wide spectrum of diversification in the Taurine group (Aparicio 1944 and Sotillo and Serrano 1985). The skull protects the brain and the sense-organs and it is also involved in feeding activities. It is formed by functionally complex morphological structures, and has been widely used for classification purposes as it keeps trace of many no skeletal tissues with related behavioral, physiological and ecological aspects (Loy 2007, Zelditch et al., 2009 and Renaud et al., 2010). Hence skull morphology would seem to be in a perfect position for the analysis of biogeographic, phylogenetic and systematic features (Loy 2007).

Available literature has been developed mainly in regard to skull linear measurements (Melgar et al. 1988, Fuentes-Ascorro et al. 2011, Salamanca and Crosby 2013 and Escobar et al., 2015), and just a few on geometric morphometrics, which represents an important tool for the investigation of phylogenetic and functional variation. Morphological integration and

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modularity are geometric morphometric concepts that refer to the covariation level between the components of a structure (Püschel, 2014). Morphological modules are those structures that have components that strongly covary, which in turn are relatively independent to other modules (Püschel, 2014). Morphological integration is instead, the coordinated morphological variation of a functional whole (Püschel, 2014).

The goal of this paper is the description of anatomic features of some cattle groups of different origin by applying geometric morphometrics methods to study integration and modularity and specifically addressing two questions: (1) Are different shape skull changes associated to different taurine groups?; (2) Which skull modules are involved? The analyses presented herein represent one of the first approaches of geometric morphometrics with this goal for domestic taurines. Although a systematic cattle classification was proposed in 1995 by Felius (Felius et al. 2011), which emphasized the geographic origin of breeds, largely in agreement with biochemical and molecular genetic analyses, this research does not intend to classify breeds, but rather consider anatomical changes among bovine domestic populations, from a strictly descriptive point of view. The information provided here may be also relevant for a better appreciation of the value of local breeds, often better adapted to their environment and more suitable for extensive management.

Materials and Methods

Sample composition

The samples were composed of adult individuals belonging to three geographical groups ("Occidental Europe, Oriental Europe and African). Occidental European set (n=30) included a variety of continental breeds for meat purposes (Pyrenean Brown, Charollais, Limousine, etc.). These skulls were collected specimens from the Department of Animal Science in the School of Agrifood and Forestry Science and Engineering, University of Lleida, Catalonia, Spain. A second set of 6 individuals of Greece area was referred to as the Oriental European group, belonging to long-horns breeds. These skulls were from the Faculty of Animal Science and Aquaculture, Agricultural University in Athens (Greece). Third set was composed exclusively of Kuri cattle (n=10). These skulls were from the Department of Veterinary Anatomy, University of Maiduguri,

Nigeria. Kuri breed is from lake Chad belonging to West African Humpless Longhorns group (Porter, 1991). It is a tall taurine (135 cm at the withers), heavy-bone with gigantic horns, sometimes described as "bulbous" horns, which are light and porous (Porter, 1991). A note on this studied African breed: increased anthropogenic pressure on the environment leading to habitat loss, as is the case for the Chad lake area, requires fast and precise ethnodiversity assessments and therefore solid morphologic knowledge of this breed.

All skulls exhibited a normal gross craniofacial morphology. As study was done on collected bones in existing collections, authors considered not necessary an ethical agreement.

Obtaining images and Procrustes coordinates

Each skull was photographed on dorsal view using a digital camera. Crania were always oriented similarly and parallel to the lens plane. Thirteen LM were chosen to study the morphology (Fig. 1), the x and y coordinates being digitized with tpsDig v. 2.26 (Rohlf, 2010). To test repeatability pictures were digitized twice by the same person. Replicated measurements of the x and y coordinates of all landmarks exhibited <12.5% error.

The resulting coordinates were subjected to a two-dimensional generalized Procrustes analysis, which removes all the information unrelated to shape (Gower 1975). Analyses were done on the symmetric component of shape variation.

Statistical procedures

The effect of allometry was verified using the multivariate regression of shape (Procrustes coordinates) on size (\log_{10} -transformed CS), with 10,000 random permutations. CS was the square root of the sum of squared distances of all the landmarks of an object from their centroid (center of gravity, whose location is obtained by averaging the x and y coordinates of all landmarks) (Webster and Sheets 2010). The covariance matrix of the residuals from the multivariate regression with size-corrected data was performed to analyse modularity after removing the influence of allometry. To characterize the patterns of integration between both modules we used PLS analysis (Klingenberg, 2014). Traditionally the skull has been divided in two modules based on their different developmental origins: the splanchnocranium and the neurocranium (Püschel, 2014). Thus the hypothesis of landmarks partitioning of the skull into these two modules (Klingenberg 2005)-splanchnocranium for LM 1 to

4, and 10 to 12, and neurocranium for LM 5 to 9 and 13- was applied. The boundaries of two skull modules were tested by comparing the *RV* coefficients among alternative partitions of the configuration into subsets of landmarks. The *RV* coefficient describes the degree of covariation between sets of variables relative to the variation and covariation within sets of variables (Adams, 2016).

Finally, a CVA was done independently for both modules. For it, pairwise Mahalanobis distances between groups were computed, and the significance of these distances was assessed through permutation tests, with 10,000 permutation rounds. All morphometric analyses were performed on MorphoJ v. 1.06c package (Klingenberg, 2011). Confidence level was established at 0.05.

Results and Discussion

Allometry and modularity

The multivariate regression of the Procrustes

coordinates on CS showed that allometry was statistically significant ($p=0.024$), so the relationship between skull shape and size was quite clear (Fig. 1). Log_{10} -transformed skull size accounted for 6.68% of the total shape variance. Shape changes were associated mainly to temporal line and zygomatic process. The two-modules *RV* coefficient showed an integration of two modules ($RV=0.466$, $p=0.032$).

Integration of neurocranium and splanchnocranium

PLS1 accounted for 77.6% of the total squared covariance between neurocranium and splanchnocranium; singular value=0.00063941, $p=0.080$. Second PLS axes (PLS2) accounted for 15.5%; singular value=0.00028580, $p=0.065$ (Fig. 2). Correlation between both modules was low ($r=0.418$) and deviated from the correlation expected for random two-module partition of landmarks ($p=0.114$). Maximum scores of PLS1 associated to temporal bones and zygomatic processes (Fig. 3).



Fig. 1. Dorsal view of the skull. Thirteen landmarks (LM) were selected, corresponding to the neurocranium (LM 1 to 4, and 10 to 12) and splanchnocranium (LM 5 to 9, and 13). No landmarks on horns were studied.

1. Occipital protuberance; LM placed at the midline of the most caudal border of the dorsal surface of the skull.
3. Left temporal line; LM placed at the middle of the left temporal line.
4. Left zygomatic process of frontal bone; LM placed on the most lateral aspect of the left zygomatic process of frontal bone.
5. Left Facial tuber; LM placed on the lateral edge of the left facial tuber.
6. Left nasoincisive suture; LM placed on the lateral end of left nasoincisive suture as viewed dorsally.
7. Rostral end of the interincisive suture; LM placed at the most rostral end of the interincisive suture.
8. Right nasoincisive suture; LM placed on the lateral end of right nasoincisive suture as viewed dorsally.
9. Right Facial tuber; LM placed on the lateral edge of the right facial tuber.
10. Right zygomatic process of frontal bone; LM placed on the most lateral aspect of the right zygomatic process of frontal bone.
11. Right temporal line; LM placed at the middle of the right temporal line.
13. Frontonasal suture; LM placed at the midline of frontonasal suture.

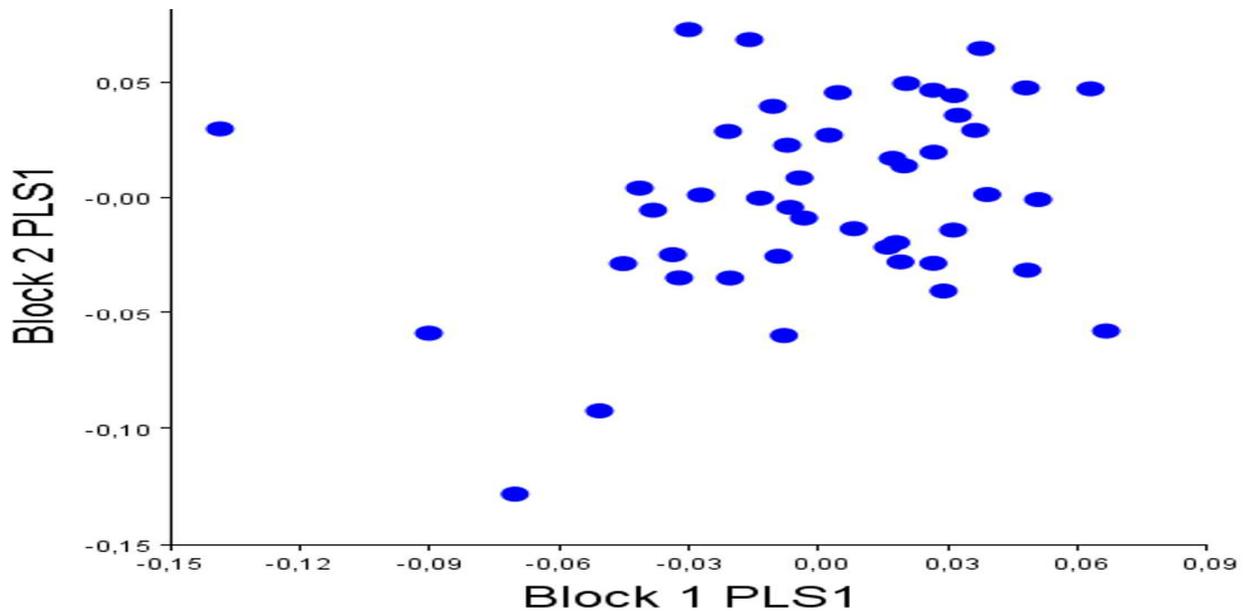


Fig. 2. Distribution of bovine specimens in the scatterplot of PLS1: variation within neurocranium (Block 1) is presented at x -axis, and variation within splanchnocranium (Block 2) is at y -axis, for corrected size. First PLS axes (PLS1) accounted for 77.6% of the total squared covariance between neurocranium and splanchnocranium; singular value=0.00063941, $p=0.080$. Second PLS axes (PLS2) accounted for 15.5%; singular value=0.00028580, $p=0.065$.

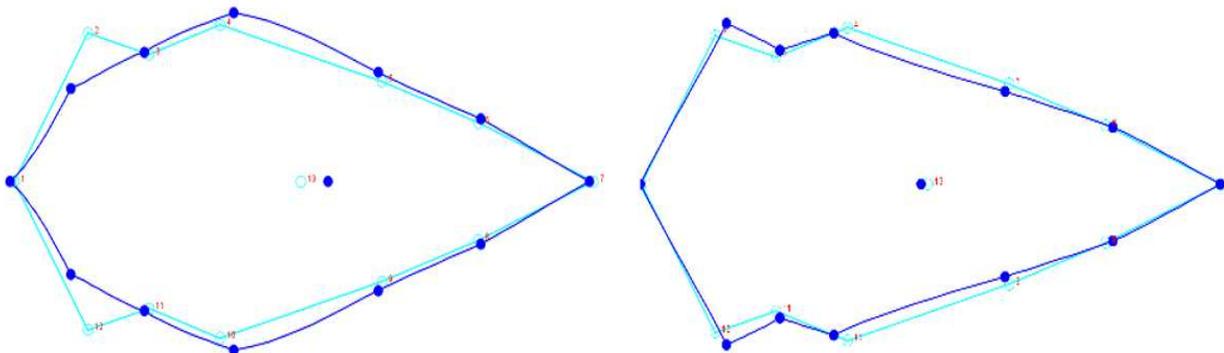


Fig. 3. Skull shape changes associated to extreme values of PLS1 scores. PLS1 are shown with dark outlines and the reference shape is shown as grey outline. No magnificated factor. Maximum scores of PLS1 were associated with temporal line and zygomatic processes.

Comparison of groups

There appeared shape neurocranial differences among European and African groups ($p < 0.0001$, 10,000 permutation rounds), but splanchnocranium differentiated only between Kuri and Occidental group ($p = 0.035$), e.g. Greek group was not differentiated from Occidental group ($p = 0.756$) and Kuri ($p = 0.493$). So shape inter-group differences were more clearly associated with neurocranium than splanchnocranium as separate modules.

Selection is a key feature in breeds' formation, since it constitutes the ability of animals to face adaptations in their environment and productive purposes, leading to a progressive increase in favourable phenotypes from one generation to the next. Plastic variation may allow individuals to survive in new conditions and ultimate morphology was a response to different environmental conditions.

Occidental European, Oriental European and Kuri breeds appear differentiated if neurocranium or splanchnocranium are taken into account, the former differentiating more clearly groups. The fact that the neurocranium and the splanchnocranium represent separated modules is confirmed by the different biological information they provide. Different horn conformation and food-processing forces directly may act on the braincase, as it is the place of attachment of horns as well as the muscles necessary for mastication. For instance, Kuris' huge horns are an adaptation to current and swimming in deep Chad lake waters. So, such a two discrete modules subdivision showed different selective changes, differences occurring mainly at the neurocranial part.

Conclusion

Occidental European, Oriental European and Kuri breeds appear differentiated if neurocranium or splanchnocranium are taken into account. The fact that the neurocranium and the splanchnocranium represent separated modules is confirmed by the different biological information they provide. Data presented in this study is interesting for the beginning of a broad trans-continental study. A more detailed craniometry plus anatomical descriptions of the bones and its components, comparing the differences found in other breeds, would be ideal for other studies. Additional morphological aspects should also be focused on bone

angulations, dental morphology and formula, and morphology of the bone orbit, just to name a few.

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